

Table 3

Effect of current velocity on four size classes of *Littorina scutulata*  
 Sample n=10 for each given value

Velocity of current (meters/second)	% snails removed by current			
	3-4 mm	6-7 mm	9-11 mm	12-13 mm
0.8	10	10	10	0
2.2	90	80	30	30
3.0	100	100	60	60

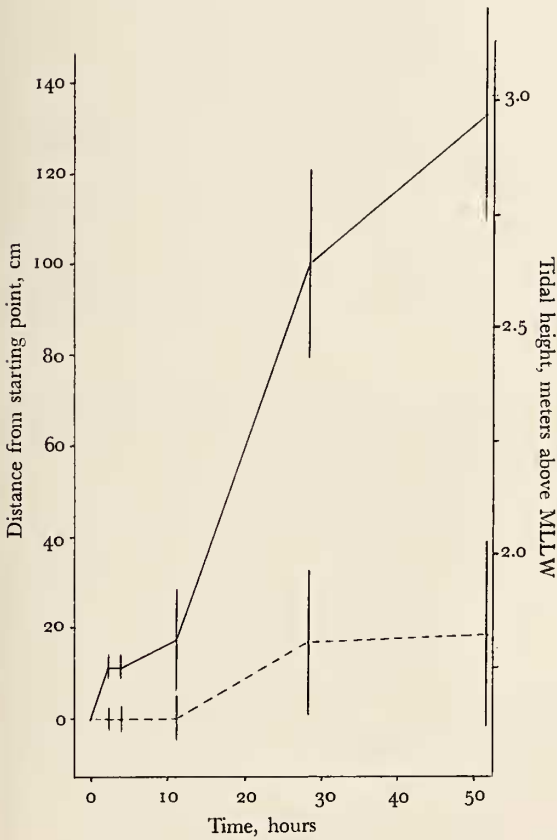


Figure 7

Vertical movements of 2 size classes of *Littorina scutulata* placed at 1.68m above MLLW; horizontal lines = mean snail heights, vertical lines =  $\pm$  one standard deviation

----- 3 - 4 mm snails  
 \_\_\_\_\_ 5 - 12 mm snails

Separation of means, student t-test:  $P < 0.001$

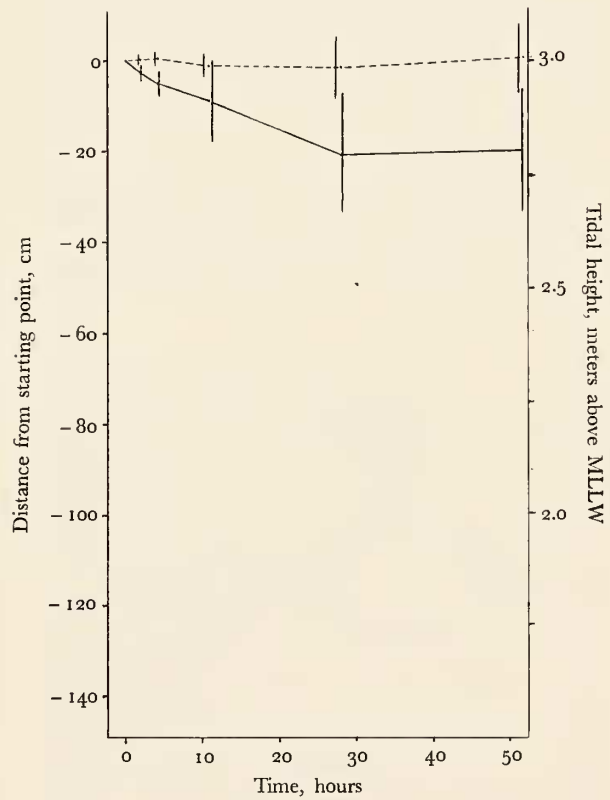


Figure 8

Vertical movements of 2 size classes of *Littorina scutulata* placed at 3.05m above MLLW; horizontal lines = mean snail heights, vertical lines =  $\pm$  one standard deviation

----- 3 - 4 mm snails  
 \_\_\_\_\_ 5 - 12 mm snails

Separation of means, student t-test:  $P < 0.01$

holes too small for large snails. Percentages are based on the recovery of 182 of the original 200 snails.

## DISCUSSION

Information collected from vertical transects located on Bodega Head does reveal a gradient in shell size within the intertidal range of *Littorina scutulata*. Contrary to the suggestions of VERMEIJ (1972), this study indicates that the shell of *L. scutulata* tends to increase in size in an up-shore direction; progressively larger snails are found with increasing tidal height. Nevertheless, the actual causes of such size-class distributions are less apparent.

In laboratory investigations, mortality due to the rigors of the physical environment fails to completely explain the observed distribution of *Littorina scutulata*. BOCK & JOHNSON (1967), BOYLE (1969), and WOLCOTT (1973) have argued that osmotic factors may limit invertebrate distributions, especially on the exposed rocks of the upper intertidal zone. Presumably, the effects of freshwater and hyperosmotic solutions are greatest at the upper limits of *L. scutulata*, where moderation by ocean tides is least frequent. The ability of large snails to tolerate osmotic stress better than small ones may be important to their relatively higher zonation. In the laboratory, however, all sizes of snails can survive immersion in stressful solutions for longer periods than the maximum expected exposure in their natural habitat.

Many studies have indicated that desiccation rates increase with decreased body size (DAVIES, 1969; BOYLE, 1970; FOSTER, 1971; WOLCOTT, 1973), and that desiccation of smaller individuals at the upper limits of distribution may cause size-specific zonation. Desiccation rates of *Littorina scutulata* under the conditions of this investigation show the same size related variation as found in previous studies, but data suggest that the size effect is most pronounced during the early evaporation-limited period of desiccation. In smaller snails, a greater portion of the total body water is lost at this time (Figure 6), and this may result in earlier mortality if, under prolonged exposure, water loss should reach critical limits. The results obtained for *L. scutulata* suggest that desiccation may set the upper range of each size class, thereby creating an upshore increase in snail shell size.

The degree to which laboratory experiments can reproduce natural conditions of wave shock is uncertain, but the effect of water currents appears to be the selected removal of smaller snails of *Littorina scutulata*, although NORTH (1954) found the opposite trend to be true of *Littorina planaxis* Philippi, 1847. If dislodgement by wave action is a range limiting factor, larger *L. scutulata* would be expected to occupy broader zones than smaller snails, on the basis of experiments carried out during this study.

Yet, when 100 large snails (10–12 mm) and 100 small snails (3–4 mm) were released in the field, no significant difference was found in the number of snails lost after more than 2 days (90% of large and 93% of small snails recovered). If wave impact accounts for the missing *L. scutulata*, then the smaller snails apparently compensate for their greater susceptibility by crawling into suitable shelter.

Thermal lethal limits seem to be a characteristic of the entire species rather than a size related tolerance. Such is the case in this study on *Littorina scutulata*, and in evidence presented by WOLCOTT (1973) on limpets. Wolcott has implied that desiccation and thermal tolerance are closely related, in which case, the combined effect may result in size-specific zonation in the high intertidal zone. However, on the basis of thermal lethal limits alone, any size of *L. scutulata* could theoretically live anywhere within the vertical range of the species.

The generally higher tolerances of larger *Littorina scutulata* to physical conditions of desiccation, osmotic stress, and wave shock may determine the ability of these snails to occupy higher levels, but the scarcity of large snails at the lower limits of the species is still left unexplained. If large snails can withstand wider environmental conditions, then they might be expected to occupy broader vertical ranges. In fact, small snails (1–4 mm) span a much greater vertical distance than large snails (5–12 mm) (Figure 4).

Other factors probably influence substantially the size class distribution of *Littorina scutulata*. Sources of suitable food may determine the vertical distribution if different sizes of snails are feeding on species of algae found at different heights in the intertidal zone. Greater predation on one size class of snails relative to the others at certain levels could result in a shell size gradient. BUSTAD (1969) has suggested that the availability of protective micro-habitats is the most influential factor in determining size distributions of *L. planaxis*, and the same may be true for *L. scutulata*. Small *L. scutulata* (1–4 mm) are often found at very low levels in the protection of barnacle beds and at very high levels in holes in the rocks, places too small for any larger snails. Small snails may be able to avoid the stresses that large snails must tolerate.

In addition to environmental factors, the role of behavioral migration can be extremely important for a mobile gastropod such as *Littorina scutulata*. Differential migration of one size group relative to the others seems to be a principal cause of zonation by size in *L. scutulata*, as shown in this investigation by the preference of large snails for a level about 2.75 or 3.00 m above MLLW. Selection of this level may be a favorable response to moisture levels, to food sources, or to availability of protective micro-habitats; the influential factors are still unclear.

The mechanisms for behavioral responses have been studied for a number of *Littorina* species. FRAENKEL (1927), as cited by FRAENKEL & GUNN (1961), demonstrated how zonation patterns in *L. neritoides* (Linnaeus, 1758) could be attained by means of relatively simple responses to gravity, water, and light. Van Dongen (1956) concluded that *L. obtusata* (Linnaeus, 1758) was attracted by scent to specific species of algae. Newell (1965) described the eye of *L. littorea* (Linnaeus, 1758) and suggested that its optical properties were adequate for form vision, which would allow visual perception of the shoreline and of algal forms. Such abilities may not be beyond the capabilities of *L. scutulata*.

The role of behavior in directing snails to specific habitats suggests several possible explanations for the zonation of shell sizes observed in *Littorina scutulata*. The situation for *L. scutulata* may be similar to the one described by SMITH & NEWELL (1955) for *L. littorea*, where the population upshore is maintained by recruitment of juveniles from very low levels in the intertidal zone. Over time, as the snails grow larger, they migrate upshore until the site-seeking behavior of the juveniles is replaced by adult behavioral mechanisms, which return the snail to the optimal level if displaced. Alternatively, the young of *L. scutulata* may settle out over the entire intertidal zone, in which case size gradients among 1-4 mm snails might result from differential growth rates or differential mortality at various tidal heights (due to lack of suitable foods, environmental stresses, intraspecific competition, etc.); adoption of the adult pattern of behavior might, then, coincide with the maturation of the small snails. However, these are only hypotheses, and complete understanding in the mechanics of the size-class distribution of *L. scutulata* must await further studies on feeding and growth, on sources of differential mortality, on juvenile settlement, and on behavioral migration.

The results of this study suggest that physical factors do not usually limit the vertical range of large *Littorina scutulata*. Rather, behavioral mechanisms keep the snails away from marginally-suitable environments. Small snails may live wherever the physical environment permits, but large snails can select levels of optimal conditions. Thus, the growth stages of juvenile snails and the development of the adult behavioral pattern may be the phenomena that appear in the gradient of shell size of *L. scutulata*.

## SUMMARY

1. This study describes the size-class distribution of *Littorina scutulata* on the intertidal shores of Bodega Head, California.

2. Physical stresses as sources of mortality were investigated in the laboratory as possible causes of zonation by size. Large snails appeared to have higher tolerances to desiccation, wave shock, and osmotic stress, while thermal tolerance was constant for all tested sizes of snails. However, physical factors alone were insufficient to explain completely the zonation by size of *Littorina scutulata*.

3. Experiments in the field revealed differential migration of large snails relative to small snails; large snails exhibited behavioral responses which kept most of them at specific tidal heights.

4. The hypothesis is advanced that, in general, the range of large *Littorina scutulata* is not limited by physical factors, but by behavior, which prompts snails to avoid marginally-suitable environments.

5. The hypothesis is advanced that the gradient in shell size observed in *Littorina scutulata* represents various stages of physical growth and of adult behavioral development.

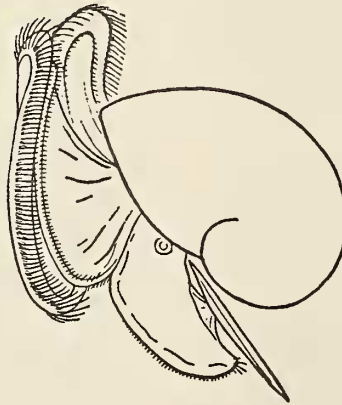
## ACKNOWLEDGMENTS

I wish to thank the instructional staff of the Bodega Marine Laboratory for the opportunity to present this study. I am especially indebted to Jon D. Standing for his advice in carrying out this entire investigation.

## Literature Cited

- BOCK, CARL E. & RICHARD E. JOHNSON  
1967. The role of behavior in determining the intertidal zonation of *Littorina planaxis* Philippi, 1847, and *Littorina scutulata* Gould, 1849. *The Veliger* 10 (1): 42-54; 8 text figs. (1 July 1967)
- BOYLE, P. R.  
1969. The survival of osmotic stress by *Sypharochiton pellisserpentis* (Mollusca: Polyplacophora). *Biol. Bull.* 136 (2): 154-166 (April 1969)
1970. Aspects of the ecology of a littoral chiton, *Sypharochiton pellisserpentis* (Mollusca: Polyplacophora). *New Zeal. Journ. Marine Freshw. Res.* 4: 364-384
- BUSTAD, KAREN  
1969. A size-frequency distribution analysis of *Littorina planaxis*: Bodega Head, Northern California. Unpubl. student rep. Bodega Mar. Labor., Univ. Calif.
- DAVIES, P. SPENCER  
1969. Physiological ecology of *Patella*. III. Desiccation effects. *Journ. Mar. Biol. Assoc. U. K.* 49 (2): 291-304 (May 1969)
- FOSTER, B. A.  
1971. Desiccation as a factor in the intertidal zonation of barnacles. *Mar. Biol.* 8 (1): 12-29
- FRAENKEL, GOTTFRIED S.  
1927. Geotaxis und Phototaxis von *Littorina*. *Zeitschr. Vergl. Physiol.* 5: 585-597
1968. The heat resistance of intertidal snails at Bimini, Bahamas; Ocean Springs, Miss.; and Woods Hole, Mass. *Physiol. Zool.* 41: 1-13
- FRAENKEL, GOTTFRIED S. & DONALD L. GUNN  
1961. The orientation of animals: kineses, taxes, and compass reactions. Dover Publ. Inc., New York. x + 376 pp.
- HAVEN, STONER BLACKMAN  
1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in Central California. *The Veliger* 13 (3): 231-248; 10 text figs. (1 January 1971)

- NEWELL, G. E.  
1965. The eye of *Littorina littorea*. Proc. Zool. Soc. London 144: 75 - 86
- NORTH, WHEELER J.  
1954. Size distribution, erosive activities, and gross metabolic efficiency of the marine intertidal snails, *Littorina planaxis* and *Littorina scutulata*. Biol. Bull. 106 (2): 185 - 197; 7 text figs.; 3 tables (April '54)
- PAINE, ROBERT TREAT  
1969. The *Pisaster-Tegula* interaction: prey patches, predator food preferences, and intertidal community structure. Ecology 50 (6): 950 - 961
- SMITH, J. E. & G. E. NEWELL  
1955. The dynamics of the zonation of the common periwinkle (*Littorina littorea* (L.)) on a stony beach. Journ. Anim. Ecol. 24: 35 - 56
- SUTHERLAND, JOHN PATRICK  
1970. Dynamics of high and low populations of the limpet *Acmaea scabra* Gould. Ecol. Monogr. 40 (2): 169 - 188
- VAN DONGEN, A.  
1956. The preference of *Littorina obtusata* for Fucaceae. Arch. Neerl. Zool. 11 (3): 373 - 386
- VERMEIJ, GEERAT J.  
1970. The *Nerita ascensionis* species complex (Gastropoda: Prosobranchiata) in the south Atlantic. The Veliger 13 (2): 135 - 138; 1 plt. (1 October 1970)
1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology 53 (4): 693 - 700
- WOLCOTT, THOMAS G.  
1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." Biol. Bull. 145 (2): 389 - 422



# An Ecological Interpretation of Nudibranch Distribution in the Northwest Atlantic

BY

DAVID R. FRANZ

Department of Biology, Brooklyn College, Brooklyn, N. Y. 11210

(3 Text figures)

THE NUDIBRANCH GASTROPODS (order Nudibranchia) of the northwest Atlantic coast of North America, excluding the Pan-Arctic fauna, comprise two distinct faunal groups: a relatively small component of endemic temperate species (FRANZ, 1970); and a larger group of 'amphi-Atlantic boreal' (amphiboreal) species. The latter, which comprise more than 70% of the nudibranchs of New England, confer a decidedly boreal cast to the northwest Atlantic fauna.

The relationships between the nudibranch fauna of New England and a series of other locations in Europe and North America are shown in Figure 1, which is a cluster phenogram based on the Dice Coefficient of similarity. Nudibranch distributional data for each location

except New England and Long Island are taken from the published sources listed in Table 1. A recent unpublished list of nudibranch records from Long Island (New York) was provided by Mr. Ron Rozsa (personal communication). The New England faunal list (Table 2) used for comparison with other locations excludes several unconfirmed species and records.

The degree of faunal overlap between all possible pairs of geographical locations (Table 1) was calculated using

a numerical coefficient, the Dice Coefficient,  $DC = \frac{2C}{N_1 + N_2}$ ,

where C is the number of species present at both locations, and  $N_1$  and  $N_2$  are the total species present at locations 1 and 2 (CHEETHAM & HAZEL, 1969). This coefficient has been used widely in zoogeographic and ecological studies, and has the characteristic of emphasizing similarity by doubling the weighting of matches relative to mismatches

<sup>1</sup> The term "boreal" is used in the framework of EKMAN (1953). Thus, European "boreal" species which extend across the North Atlantic into American waters are "amphi-Atlantic" boreal or amphiboreal species.

Table 1

Location	Number of Species		
	Total	Boreal Amphi-Atlantic	Reference
Brittany	27	6	TARDY, 1962
England	99	16	THOMPSON, 1964
Faroës	27	14	LEMCHÉ, 1938
Iceland	23	14	LEMCHÉ, 1938
Isle of Man	52	18	BRUCE, COLMAN & JONES, 1963
Long Island, New York	15	10	ROZSA, 1974—unpublished
Maryland-Virginia	9	3	MARCUS, 1972
Gulf of Naples	92	3	SCHMEKEL, 1968
Netherlands	30	16	SWENNEN, 1961
New England	29	21	FRANZ, unpublished
Norway north of Lofoten	60	16	LEMCHÉ, 1938
Norway south of Lofoten	31	18	LEMCHÉ, 1938
West Greenland	20	10	LEMCHÉ, 1941